PHENOLOGICAL OBSERVATIONS IN STEPPE COMMUNITIES WITH A CONSIDERATION OF THE MORPHOLOGY AND BIOLOGY OF PLANTS

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PHENOLOGICAL OBSERVATIONS IN STEPPE COMMUNITIES WITH A CONSIDERATION OF THE MORPHOLOGY AND BIOLOGY OF PLANTS

/Following is the translation of an article by Z. G. Bespalova and I. V. Borisova in the Russian-language journal Botanicheskiy Zhurnal (Botanical Journal), Moscow, No 9, 1963, pages 1271-1281./

With four figures

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Phenological development of plants of Central Kazakhstan has long been poorly studied. Existing investigations (Borisova and Popova, 1959; Ganetskaya, 1960) do not fully illuminate this problem. In this article, we do not aim at giving a complete picture of the seasonal development of steppe plants. Our aim is narrower -- to show characteeistics of the biology and morphology of plants which must be taken into account in making phenological observations /See Note 1/. Four years of observations at desert-steppe and two years of observations at arid-steppe stations allow us to present these descriptions /See Note 2/. Natural characteristics of the stations have been given in articles by Ye. I. Rachkovskaya (1961) and N. P. Gurichevaya (1961).

As a result of phenological observations made we concluded that there is a need for a differentiated approach to discovering and characterizing individual phenophases in plants but differ in rhythm of development, life forms, and certain other biological features: character of flowering, mode of pollination, method of dissemination.

(/NOTE 1/ The methods followed in the phenological observations have been set forth earlier by the present authors (Bespalova and Borisova, 1960).)

(/NOTE 2/ The desert-steppe station is located 40 kilometers southwest of the Zhana-Arka Station of Karagandinskaya Oblast, in the hollow-feather grass subzone of the semi-desert zone (Rachkovskaya, 1961). Phenological observations were made during 1958-1961. The arid-steppe station is located in Barankul'skiy Rayon of Tselinogradskaya Oblast, 250 kilometers south of the city of Atbasar, in the dry steppe subzone (Guricheva, 1961). Phenological investigations were made either during 1957-1958. T. A. Popova took large part in all these studies.)

The composition of steppe plant communities include, as is known, plants which differ in rhythms of seasonal development: ephemerase and ephemeroids, hemiephemeroids, slow-growing plants with a period and without a period of summer dormancy or semi-dormancy. Such a combination of plants, a result of the history of the formation of steppe communities, is responsible for a frequent change of appearances. The extent of development of any given group of plants in a given season, the ratio of the number of vegetative and generative species, depending mainly on meteorological conditions during the year, determines the appearance of the community, and also the presence or absence of a particular aspect of appearance. Although the arid and desert steppes in which the investigations were made are not distinguished by such a brilliance and diversity of views such as are characteristic of meadow and motley and feather grass steppes (Lavrenko, 1940, 1956), in individual favorable years even in the former steppes well pronounced dazzling views of flowering and fruiting feather grasses, flowering tulips, spiraea, pea trees, etc., have been observed.

The diversity of life forms is very extensive among steppe plants. We find, in the woody plant category (as defined by I. G. Serebryakov, 1962) shrub (species of the genera Karagana, Spiraea, Rosa, etc.) and semishrubs, (species of the genera <u>Artemisia</u>, <u>Astragalus</u>, <u>Atritlex</u>, etc.). Also numerous and diversified as to life forms are the perennial grasses (turf, rhizomal, bulbaceous, tuberous, etc.) and annual plants (chiefly the ephemeras). In addition, the growth forms play a large role in determining the rhythm of seasonal development of plants. We can distinguish by growth form the following plants in steppe communities: nonrosettal, semirosettal, and rosettal plants (Borisova, 1960).

We find both anemophilic (cereal grasses, wormwoods, and certain Russian thistle plants (and entomophilic plants, differing by mode of pollination. The latter can have both specialized (milk vetch (<u>Astragalus sp.</u>), pea trees (<u>Caragana sp.</u>, and toad flax (<u>Linaria sp.</u>)) or with open flowers (spiraea, giantfennel

(Ferula sp., and certain members of the cruciferae family). There is also the group of autogamic plants (chiefly ephemeras). By mode of dissemination we found the anemochores (Feather grasses, certain thistles) predominating among steppe plants, while there are sizeable groups of autochores (mostly members of the cruciferae family and pea trees) and ballists (tulips, onions, giant fennels), very few zoochores (ephedra, zhimolost' [?], and stickseed (Lappula sp.). Thus, steppe plants are also highly diversified by mode of flowering and dissemination.

All the foregoing points to the impossibility of an identical approach to such different plants when phenological observations are made.

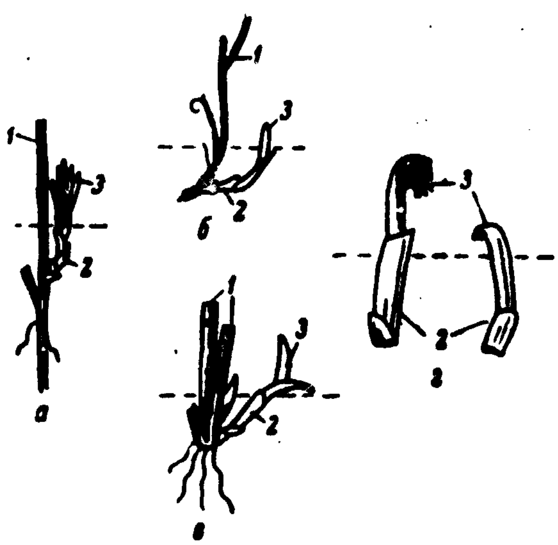

Figure 1. Aftergrowing phase (plant fragments are shown). a - sprout of Dianthus leptopetalus Willd., vicinity of the Zhana-Arka Station, 14 April 1960; b - shoot of Agropyrum pectiniforme Roem. et Schult., vicinity of Arkalyk, 3 May 1959 (figure by T. A. Popova); c - shoot of Galatella angustissima (Tausch) Novopokr., vicinity of Zhana-Arka Station, 14 April 1960; d - shoots of Ferula sangorica Pall., Koksengir, 24 April 1960. 1 - dead last year's shoot; 2 - rhisomal portion of this year's shoot; 3 - above-surface portion of this year's shoot (sprout).

We will dwell briefly on features of the seasonal developmental rhythm of plants in the arid and desert steppes.

During spring, after thawing of the snow (at the end of March, beginning or mid-April), aftergrowth of the perennial plants begins: etiolated yellowish, pinkish, or green shoots (Figure 1), which are either regeneration buds beginning growth (as in the case of Galatella, Linosyris, Dodartia, etc.) or the unfurled first leaf (as in the case of Ferula, Rheum, vegetative species of Tulipa, etc.). Apical and axillary buds unfold in shrubs and certain semi-shrubs (milk-vetch) during this time. Somewhat later (in time), if the weather is favorable, shoots of annual and perennial plants appear.

Since this period is distinguished qualitatively, not only morphologically, from the previous and subsequent developmental periods, since during this time plant nutrition proceeds as a whole through accumulated reserves of plastic [sic] substances in seed pods, rhizomes, roots, etc., we differentiate this period as an independent pherophase -- the onset of aftergrowth and the appearance of shoots. It lasts for a relatively short while, and the formation of the first real leaves already points to the transition to the following phenophase.

Evergreen plants (turf grasses, biennial plants during the second year of life, many semi-shrubs) continue to vegetate immediately after the snow leaves, therefore for them the phase of the onset of aftergrowing in the sense indicated above is absent. These plants usually have open axillary regeneration buds, and their last year's winter with green apical leaves, which after restoration of vegetation are still capable of growth and assimilative activity.

The appearance of normal green leaves, as already indicated, demonstrates the transition to the next phase -- vegetation, which evidences the presence of the active life of the plant [See Note]. During this period the aftergrowing of vegetative shoots occurs (tillering of the cereal grasses and certain other perennial grasses), aftergrowing of the rosettal leaves in plants which have perennial monocarpic shoots (di-, tri- and polycyclic). We should remember that in spite of the aftergrowth of new leaves, during the summer period of plant development simultaneous gradual withering of the lower leaves in acropetal order also takes place. This still does not mean attenuation of the vegetative phase, since the process of de novo formation either predominates over the withering process, or after certain time these processes become equalized to each other.

([NOTE]. The term vegetative phase is usually used in a dual sense: a) to denote the overall process of seasonal growth and development of plants in contrast to the state of dormancy and b) to designate one of the phenophases during the seasonal developmental cycle. In the second case the term "vegetative phase" can, must be replaced by another, but this is difficult and there is as yet o suitable term.)

In vegetative specimens this phase lasts until the onset of dessication, in generative specimens -- until the aftergrowing of flowering shoots. An interesting feature has been observed for ephedra (Ephedra distachya L.). For this plant, as observations have shown, for one or even two years in succession new annual shoots may not grow, but the plant continues to live through the assimilation of old shoots, which remain green for several years. External, visible growth and development is not present, while the vegetative phase somehow continues. The ephedra, therefore, is a distinctive evergreen plant.

For evergreen plants, especially for turf cereal grasses, during this phase the curling up of leaves of autumn generation is observed for the first time, and then leaves of the new spring generation aftergrow. This phenophase is evident for annual rosettal and semi-rosettal plants, but is in fact, very short-lived. Generative specimens of tulips, also non-rosettal plants, in contrast, avoid the vegetative phase form flowering shoots after the aftergrowing period.

The next phenophase which is observed in all annuals and perennial non-rosettal plants without exception and only in generative specimens of semi-rosettal and rosettal perennial plants is the phase of the aftergrowth of fruiting shoots (shooting for cereal grasses, stemming according to A. P. Shennikov) /See Note/.

(/NOTE/. A. P. Shennikov (1927) regarded the appearance of extended shoots as a subphase of the vegetative phase.)

During the course of this phenophase essential changes in the appearance of the plant take place, especially in semi-rosettal plants, -- gradual aftergrowth of the flowering shoots occurs, and immediately we note differences between the vegetative and generative specimens during a given year (Figure 2). This of course is a new developmental stage in the life of the generative specimens.

In semi-rosettal and non-rosettal plants this phase lasts for a long time (usually more than a month, and sometimes as many as two and even three). For rosettal plants, in contrast, it passes rapidly; here for species with extremely specialized shoots (*Spiraea*, *Caragana*, *Astragalus arcuatus* Kar. et Kir., *A. testiculatus* Pall.), for which buds have formed already in the sprouts, and this phenophase is in factual terms very difficult to distinguish, for it is very short-lived.

For non-rosettal plants (*Linosyris tatarica* (Less) C. A. M., *Galium ruthenicum* Willd.) during very dry years some of these specimens, even all or most of them do not form flowers, but still all their vegetative shoots are potentially generative and wither by winter as do ordinary flowering shoots, that is, the seasonal development for these specimens and at the stage of aftergrowth of the flowering shoots, without entering budding and flowering.

Aftergrowth of flowering shoots terminates with the formation of flowering and appearance of buds in plants with single or limited numbers of flowers, and the plants enter the budding period.

Since we distinguished the aftergrowing phase of flowering shoots, the budding phase (earing in cereal grasses) was somewhat limited for our purposes compared with the extent of this phase held by other authors (Beydeman, 1954, 1960). It encompasses the period of bud formation, when the growth of individual parts of the flower occurs, and then the coloration of the petals. According to G. D. Frolova (1950), two subphases can be distinguished in the budding period: [See Note] 1) compact buds and 2) loose buds. The loose bud subphase is usually shorter compared to the compact bud subphase; in some cases, the opposite is the case, or they are of equal duration. For example, the first subphase for Tulipa patens Agarh. lasts 10-15 days, and the second only two-three days. The ratios in time for Ferula songorica Pall. between the subphases are approximately equal: from the time the bractal leaf unfurls until the complete formation of the inflorescence 5-6 days elapse (the buds during this period are hard and green), but it flowers in 13-15 days (Figure 3).

([NOTE] A. P. Shennikov (1927) also distinguished two subphases in the budding phase: 1) the young buds and 2) ripe buds.)

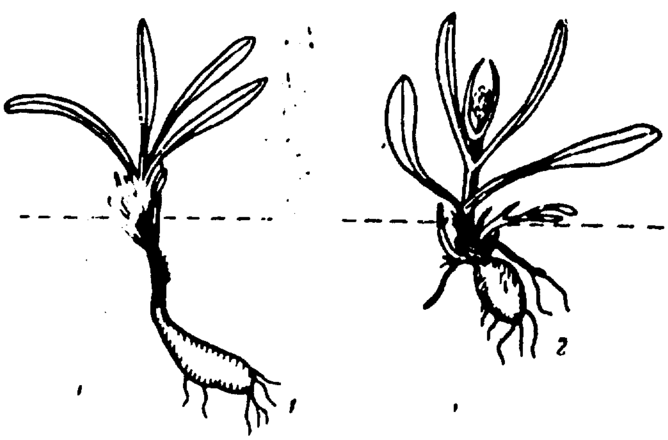

Figure 2. Generative and vegetative specimens of Valeriana tuberosa L., vicinity of Arkalyk, 1 May 1959 (Figure by T. A. Popova).
1 - vegetative specimen in vegetative phase: 2 - generative specimen in phase of flowering shoot aftergrowth.

We must turn our attention to this phase in sagebrush. This plant has still another intermediate link between aftergrowth of flowering shoots and budding proper -- formation of calathides, which precedes bud formation. Ye. A. Mokeyeva (1945) designates this period as "pseudo-budding" (Figure 4). The budding phase in sage brush accordingly lasts very long -- 1.5-2 months.

It is often very difficult to pinpoint the moment of transition from aftergrowth of flowering shoots to budding, since this transition often is very gradual, especially in plants with complex inflorescences. This stems from the fact that the growth of a flowering shoot in such plants does not end at the outset of formation of buds, which form gradually as the apex of the inflorescent continues its aftergrowth. In this case, the aftergrowth of flowering shoot phase has been taken by the present author as terminated by the end of the formation of the first compact buds, since we have not found here a more or less clear-cut division between aftergrowth of a flowering shoot and the onset of budding.

When the first flower unfolds or when pollination begins (for wind-pollinated plants without a sufficiently developed perianth), the flowering phase begins. The character is flowering is dissimilar for different species of plants, since it depends on the mode of pollination (anemophilia, entomophilia, or self-pollination). The duration of flowering is also dependent on other factors: weather, age of plant, type of inflorescence.

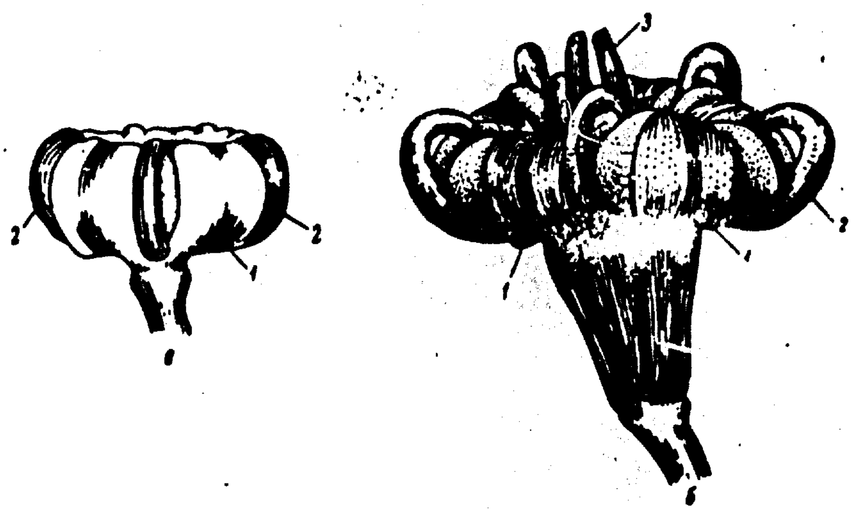

Figure 3. Budding phase in Ferula songorica Pall. (Figure by G. N. Uvarov). a - subphase of compact bud; b - subphase of loose bud. 1 - petal; 2 - stamen; 3 - pistil.

The individual petals in wind-pollinated plants flower during several hours, after which it curls up and by the following day no longer unfurls. We must recall therefore that in conducting phenological observations that flowering of anemophilic plants is restricted to a definite time of day and that pollination here occurs quite rapidly. For example, cereal grasses bloom early in the morning, during the day, or during evening, that is, in three periods (three waves according to A. N. Ponomarev, 1954; and Z. G. Bespalova, 1961). Flowers of the sage brush bud forth all day long, but most of the flowers blossom during the hours between 8 and 9 in the morning.

Pollination of such plants as Kochia prostrata (L) Schrad, Camphorosma monspeliacum L., and saltbush Atriplex cana C. A. M. occurs toward noon (between the hours of 10 and 12 in the morning).

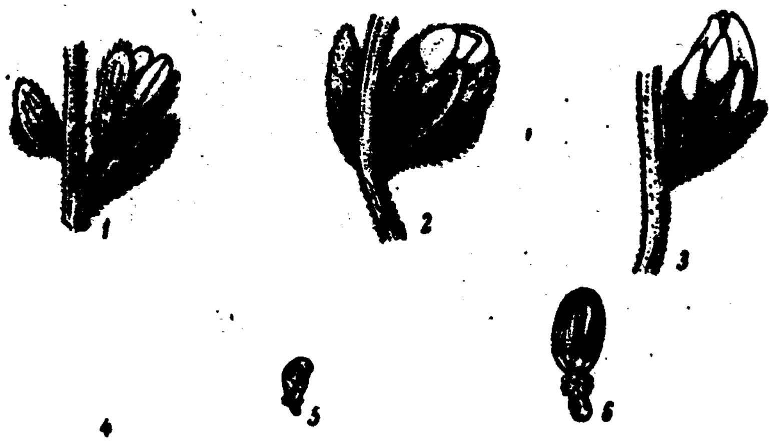

Figure 4. Budding phase in Artemisia lercheana Web. 1-3 -- formation of calathide (26 August, 17 September, 8 October); 4-6 -- development of flower (during the same periods).

The individual petal of entomophilic plants blossoms up to the hours of 5-6 in the afternoon and later. The duration of flowering of a single specimen of a given species or its entire population, as already remarked, depends on weather conditions during the flowering period. Cold weather (low air temperatures, cold wind, rain) considerably delay both the onset of blooming as well as flowering itself (Bespalova, 1962). On humid or rainy days, flowering is generally curtailed. Tulips react quite decisively to moisture: their flowers instantly curl up if the relative humidity exceeds 90 %. Sage brush flowers in humid or rainy weather do not unfurl. During periods of drought plant development occurs very much more rapidly than during ordinary years, blossoming and flowering of plants is accelerated. For example, the Kirgiz feather grass Stipa kirghisorum P. Smirn. during the very wet year of 1958 blossomed in 10 days (from 1 to 11 June) and during the dry year of 1961 in only 6-7 days (from 5 to 11-12 May).

This plant reacts very quickly and delicately to change in weather at the end of the shooting phase, during earing and flowering of sage brush. Intense drought during spring or during the period of flower formation gives rise to cleistogamic flowering in these plants. During some years, different generative shoots could be seen in a single sward of sage brush: some of them were cleistogamic, others chasmogamic (normal) flowers. This difference was due to the sudden change in weather during the flowering period. If the plant had begun to flower normally, and then a drought quickly set in (hot, dry winds blowing), the shoots which had not been able to firm up before the drought began to flower cleistogamically; and, in contrast, if after the dry weather rain fell, the cleistogamic flowering was replaced by normal. It is very difficult to observe cleistogamic flowering in the sage brush. I. N. Beydeman (1960) writes that "for cleistogamic plants, the onset of flowering must be taken as the period when the anthersopen up" (page 344). The onset of pollination in these flowers can be established only by opening them, but to look at all flowers in succession (for a quantitative estimate) is impossible; this means that the percentage of flowering specimens and the character of flowering (onset, climax, or blossom fall) at a given moment can therefore not be determined. It is probable that this impasse can be breached by looking for external characteristics pointing to the onset of cleistogamic flowering. That cleistogamic flowering has already occurred can be judged from the yellowing of the apex of the covering bractal leaf. It must also be remembered that shoots bearing cleistogamic flowering differ from normally flowering shoots quite well externally -- they grow very slowly (late-ripening) and appear to remain quite protractedly in the phase of "shooting" /See Note/.

(/NOTE/ It need only be recalled that this is the same mode followed by generative shoots damaged by rust at the onset of development, and also (according to the observations of L. V. Arnol'di) shoots damaged by insects.)

The character of inflorescence affects the duration of flowering differently in different plants. In some plants which have large numbers of flowers in their florescence (up to 3500 in the Ferula dzhungarskaya) flowering occurs quickly and hence rapidly (during 10-12 days); in other plants which have considerably fewer flowers in the inflorescence, flowering lasts for a month to a month and a half. This is most likely due to the flowering process and the overall biology of the plant. For example, in such plants as Kochia, Camphorosma, Spiraea of the Chenopodiaceae family, flowering begins with the unfurling of the stigma, and pollination proceeds only 2-3 weeks after this, when by this time the stigma has already shriveled up. Extended, even discontinuous flowering (Grudzinskaya, 1960) distinguishes certain representatives of the Cruciferae family Erysimum, Sisymbrium, Syrenia), and also species of the genera Flomis, Dianthus rigidus M. V., and others. Because of this fact, it is convenient to distinguish intermediate subphases, as many authors have done, for example Ye. M. Lavrenko (1952) for the period of transition from flowering to fruiting (FF).

Withering of the flower corollae points to the transition of the plant to fruiting. This transition is easily seen in plants with open or with large flowers. For example, 2-3 days after the pollination of the tulip the corollae bends and the ovary swells visibly. The corollae of the pea tree Caragana balchaschensis (Kom.) Pojark. falls off only on the fourth-sixth day following fruiting, when the onset of pod formation is readily visible. It is more difficult to observe the transition to fruiting with plants with small and with closed flowers. Only by the 5th-6th day, in the case of cereal grasses, can touch be used to determine whether fruits have been conceived or not.

The duration of the fruiting phase is different for different plants. Almost always this phase compared with other generative phases (budding, flowering, dissemination) is longer (from 2 weeks to one month and more). This duration also depends on weather. In the case of ephemera, ephemeroids, and hemiephemeroids, fruit formation is accompanied by gradual withering of the flowering shoots themselves, which by the middle or end of this phase become completely dry. We believe it important to note in these plants the moment of withering of the flowering shoots, since it points to change in moisture conditions, to the intense dessication of the upper soil horizons. Accordingly, we distinguish two subphases in the fruiting phase of quick-growing plants: 1) fruiting, green stem; 2) fruiting, dry stem.

Often after the flowering phase vegetation begins again, since the fruit for some reason or other has not become infructescent. For entomophilic plants this is related to the lack of a pollinator, especially, if the plant is pollinated by one species of insects, for example, toad flax Linaria incompleta Kupr. Usually during the cold weather of the year, bees and other insects are greatly hampered, and sometimes spring conditions are such that many species of pollinating insects are not developed. The absence of a fruiting phase can also stem from the fact that when the weather is unfavorable certain parts of the flower are not well developed in time. This can often be observed in cereal grasses: sheep's fescue Festuca sulcata Hac., Koeleria gracilis Pers., sage brush, and also tulips, pea trees, and other plants for which sometimes given abundant pollination there is not infructescence. In this case, there is pseudo-fruiting in cereal grasses and thereupon, pseudo-dissemination occurs externally "as usual," only very greatly "protracted," and in other plants (with more or less large flowers) it immediately becomes clear that there will be no fruit.

Very strong wind during pollination of anemophilic plants quickly blows away pollen, which considerably reduces the percentage of pollinated flowers. In addition, insects damaging the fruit inflict great harm on plants. Sometimes, the percentage of damage especially in legumes become so high that the fruiting phase in these plants in fact never terminates and they do not make the transition to dissemination, for their fruit always or almost always will prove to be shriveled. Such events that are catastrophic for plant generation are observed as hailing or devouring of flowers and inflorescences (both during the flowering stage as well as in the fruiting phase) by rodents or other mammals (marmots, field mice, conies, saigas, etc.), which also must be taken into account.

Plants for which there is infructescence and fruiting proceeded normally, makes a transition to dissemination (dropping and scattering of fruit). The duration of this phase depends, in addition to weather conditions, on the mode of dissemination. Wet weather, especially rain, delays fruit fall. For example, during wet weather the calatherides of the sage brush, the seed pods of the tulip, spirae, and other plants are covered tightly, and only opening them will show that the seeds are ripe and their dissemination has already occurred.

Shattering of plant embryos [zachatki] occurs very rapidly in anemochore plants, especially euanemochores. Dissemination of autochores also occurs fairly rapidly. The seed of ballists [See Note] are shed more slowly. For their dissemination, sufficiently forceful wind or some mechanical factor is required. Dry, windy weather accelerates shattering of plant embryos for all plants (except for zoochores). For example, shattering of seed of Tulipa patens during the moist year of 1958 lasted to 25 August, while during the very dry year of 1961 it had already ended by 10-12 June. The character of propagation of plant embryos very strongly affects duration of dissemination in ephemeras and ephemeroids, since it takes place when these plants are in dry stem.

([NOTE] Ballists are plants which have adaptations impeding self-directed shattering of plant embryos, the scattering of which becomes possible only upon cracking open of elastic stems, floral shoots, and flower stalks (Levina, 1957).).

It is difficult to determine the duration of the disseminatio. phase in plants of the specialized life form of "tumbleweed." We can establish only the time of rupture of the generative shoots from the plant, while dissemination in this way is not concluded, but continues for some further time. Special observations are needed in order to discover the duration of the entire period of scattering of fruit.

After complete dissemination, long-vegetating plants for which there is no period of summer dormancy continue to vegetate. Ephemeras, ephemeroids, and hemiephemeroids, as already remarked, are disseminated in the dry state. For these plants, even during the time of scattering of plant embryos, essentially the dormancy phase continues, which lasts until the following spring, and only in some plants -- to fall.

For long-vegetating plants which have a period of summer dormancy or semidormancy, following dissemination or after some time drying begins again. This phase is observed also in long-vegetating plants which have not summer dormancy period, at the end of vegetation, before covering by snow. Drying proceeds gradually, therefore the start of this phase is difficult to determine. As to characteristics of the vegetative phase, we have already indicated that at some point, the growth of new apical leaves is accompanied by gradual drying of the lower leaves, but growing still predominates over withering. In this period, when the drying of the leaves becomes evident on a massive scale, and no new leaves are seen to be formed, vegetation begins to slacken. In accordance with the foregoing, we regard the onset of drying to be the state of the plant when most of the leaves on the vegetative shoots have withered, and the remaining leaves are drooping (yellowing or reddening). Thus, in sod cereal grasses, the state of semidormancy begins when the tip of the apical leaf begins to wither, and the one-two leaves situated below are already completely dry or almost so [See Note]. For shrubs, the drying phase begins usually with the blossoming of the leaves and ends in the gradual leaf fall.

([NOTE] From one to three leaves develops on each shoot of sod steppe cereal grasses during spring, and only four-five leaves (on an average) are formed during an entire season.)

Drying as a phenophase in some plants ends with the transition to the state of summer or winter dormancy, while in others -- with the restoration of vegetation. This last state is especially characteristic of steppe sod cereal grasses, for which the semidormancy period (less often full dormancy) begins with the onset of dry weather wherein usually at the beginning, middle, or end of July) and continues until the rains come (at the end of August-September). In very wet years (1957, 1958, and 1960) the semidormancy period for these plants was weakly in evidence while in dry years (1959, 1961) marked parching was observed. During the semidormancy period, intense but not complete drying of the leaves takes place, assimilation and transpiration continues (Yang Bao-chien, 195?; Zalenskiy, Shtan'ko and Ponomareva, 1961; Sveshnikova, 1962).

The phase of full summer dormancy is due to the loss of all the assimilating parts of the plant (leaves and stems in grasses, and leaves in shrubs). Only the buds and lignifying shoots located above the surface of the soil remain living, along with grassy and lignifying shoots with restoration buds located in the soil.

Autumn aftergrowth, replacing the period of summer dormancy or semidormancy, takes place after adequate soaking of the soil and depends entirely on weather conditions. During a dry autumn it takes place very slowly, while in hot and moist autumn weather -- very intensively. During favorable years, in addition to secondary vegetation, secondary aftergrowth of flowering shoots, budding, flowering, fruiting, and dissemination [See Note] are also observed. In these instances, generation most commonly ends in flowering, usually very scanty, but in other years massive. The fruit after secondary flowering are not always infructed (there are no pollinators or the individual parts of the flower are underdeveloped). Thus, in the dry steppes during 1959, massive cleistogamic flowering of the feather grass Stipa lessingiana Trin. et Rupr. was observed, but no infructescence. Secondary flowering of Spirea occurs almost annually. During 1961, it was very early and ended in fruiting (normal seed were infructed).

([NOTE] We regard flowering as secondary only in the case when during autumn new specimens or new shoots which had not yet flowered during the year break out in bloom. If, however, the shoot had flowered during spring or summer, and in autumn only continuation of flowering was observed usually by way of axillary (side)shoots, we call such flowering supplementary (Bespalova and Borisova, 1960).

Winter dormancy, as is known, can be obligatory and forced. Among steppe and semidesert plants, there is a fairly large group of evergreen species (sod cereal grasses and certain representatives of motley-grass, many semishrubs) which during winter are in the state of forced dormancy. Another group of plants winter only in the form of buds, bulbs, roots, and other organs of restoration (without leaves being retained).

These are certain features of the biology and seasonal development of steppe plants of Central Kazakhstan.

All the foregoing shows that in making phenological observations we are inclined to differentiate several more phenophases than has been done by other authors (Shennikov, 1927; Shalyt, 1947; Beydeman, 1954).

We distinguish ten principal phenophases (below they are denoted by Roman numerals), and, moreover, we further subdivide the generative phenophases into subphases (below we give these arabic numerals).

Phenophases

I. Onset of aftergrowth and appearance of sprouts.

II. Vegetative.

III. Aftergrowth of flowering shoots (shooting in the case of cereal grasses).

IV. Budding (earing in the case of cereal grasses).
   1. Budding (onset) - compact buds
   2. Budding (climax) - loose buds
   3. Budding + flowering (onset of flowering).

V. Flowering (pollination in anemophilic plants).
   1. Flowering + budding (end of budding).
   2. Flowering (climax).
   3 Flowering + fruiting (beginning of fruiting).

VI. Fruiting (formation of fruits). [See Note]

([NOTE] For short-growing plants other subphases must be distinguished: 1) fruiting, green stem; 2) fruiting, dry stem.

   1. Fruiting + flowering (end of flowering).
   2. Fruiting (climax).
   3. Fruiting + dissemination (onset of dissemination).

VII. Dissemination (shattering of fruits). [See Note]

([NOTE] For short-growing plants this phenophase occurs during dry stem period).

   1. Dissemination + fruiting (end of fruiting).
   2. Dissemination (climax).
   3. Dissemination (end).

VIII. Drying (semidormancy).
IX. Summer dormancy.
X. Winter dormancy

In addition to the principal phenophases, additional (postgenerative vegetation, supplementary budding, supplementary flowering, etc.) and secondary phenophases (secondary aftergrwoth of flowering shoots, secondary budding, secondary flowering, etc.) are also distinguished. Dividing the vegetative phase into three independent phenophases appears necessary since these three periods of phenological development are qualitatively distinct and are well differentiated morphologically.

The number of phenological phases which each specific species or definite biological group of plants passes through annually depends on the origin of the plants, and for a particular season -- on weather conditions. In other words, plants belonging to different biological groups can, in their seasonal development, pass through a different number of phenophases. From this, stems the need for a differentiated approach in distinguishing individual phenophases in different groups of plants and an individual approach when making phenological observations.

Similar to the approach of A. P. Shennikov (1927) and I. N. Beydeman (1954, 1960), we believe it obligatory in phenological investigations to estimate the number of adult specimens passing through a given phenophase (Bespalova and Borisova, 1960). This enables us not only to find out the ratio of specimens in the generative and in the vegetative state for a given year, but also the character of arrival of each phenophase (sudden or gradual transition to the following developmental phase). The character of this transition depends not only on weather but also on the age composition of the population of species constituting the community. Our investigations have shown that the entire cycle of seasonal development in young specimens proceeds somewhat more rapidly than in adult plants. Related to this in large degree is the difference in time in the onset of the same phenophases, which has been observed in populations of plants of a given species in communities (phenological nonuniformity of population, according to I. A. Grudzinskaya, 1960). Thus, the juvenile plants of Ferula songorica dry up 2-3 weeks earlier than do the adult vegetative specimens of this species. In wet, but hot years, the difference is especially visible in the passage by specimens of different ages through different phenophases, while the dry years the difference is reduced. In addition, different biological groups of plants pass through the same number of phenophases at different times and at different rates, which is determined by their origin.

A differentiated approach in phenological observations makes it possible to reveal in more detail characteristics of seasonal rhythm of development of each individual species of plant and different biological group.

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